

TRILOBITES AND THEIR TRAILS IN A BLACK SHALE: EARLY CAMBRIAN OF THE FLEURIEU PENINSULA, SOUTH AUSTRALIA

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Summary

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An Early Cambrian trilobite from the Normanville Group in the Sellicks Hill area, Fleurieu Peninsula, South Australia is here identified as *Ivshiniellus briandallyi* sp. nov. The trilobites occur in 'black shale' in close stratigraphic proximity to a bedding-plane surface showing trails made by large trilobites. The environment was below storm-wave base and the traces indicate that the black shale deposited in water sufficiently well oxygenated to support large metazoans with a presumed oxidative metabolism. Black coloration in shales may not be taken as a necessary indication of anoxic bottom waters.

KEY WORDS: new species, conocoryphid trilobite, trace fossils, black shale, Cambrian, South Australia.

Introduction

Jago *et al.* (1984) reported the first discovery of trilobite remains in the Early Cambrian Normanville Group on Fleurieu Peninsula, South Australia. They described two specimens of a conocoryphid trilobite from the Heatherdale Shale in the Sellicks Hill area (Fig. 1), but considered the material so poorly preserved as to preclude formal description. While exploring the same site during late 1984, one

of us (P.H.) discovered a spectacular trace fossil made by an arthropod. Further searching revealed two more body fossil remains of trilobites. This paper reports these new discoveries.

Of the new trilobite remains, one shows the cephalon and anterior thorax and the other is a fragmentary thorax. They were discovered on surfaces that had split open to the weather, and the very incomplete specimen is preserved essentially as a ferruginised film. The more complete individual, an external mould, resembles specimen SAM P24321 described by Jago *et al.* (1984) and provides

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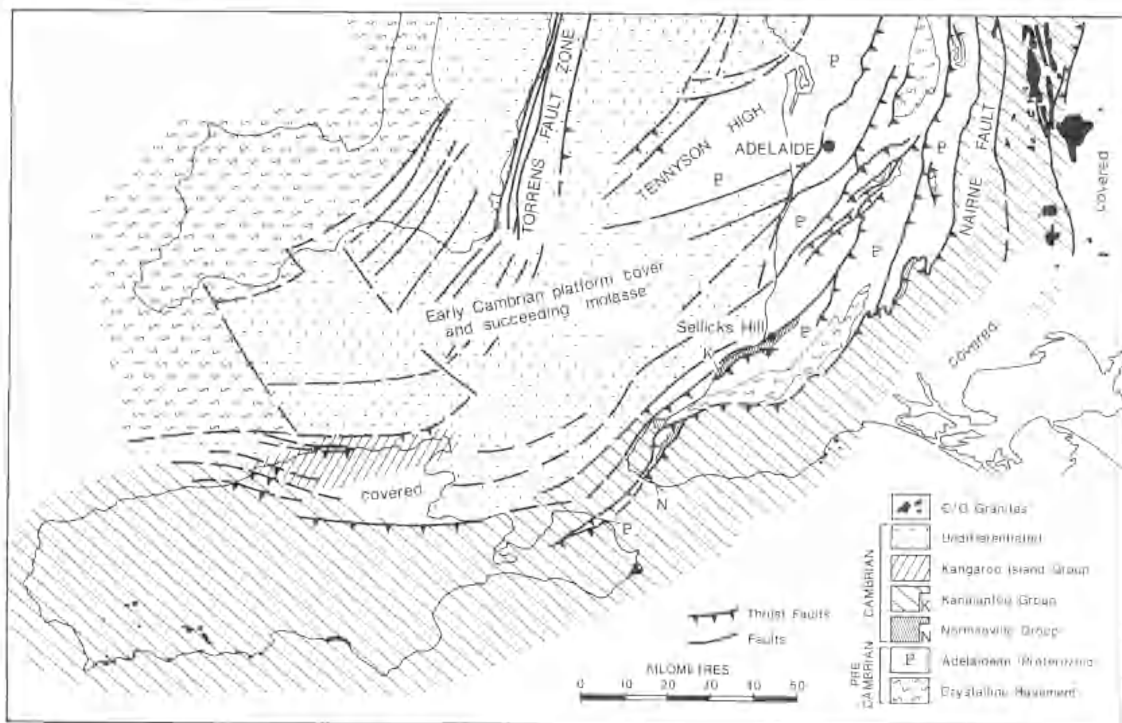


Fig. 1. Locality map showing find of trilobites and trace fossils at Sellicks Hill, and the placement of this discovery in relation to the framework of the Adelaide Fold Belt and adjacent foreland basin.

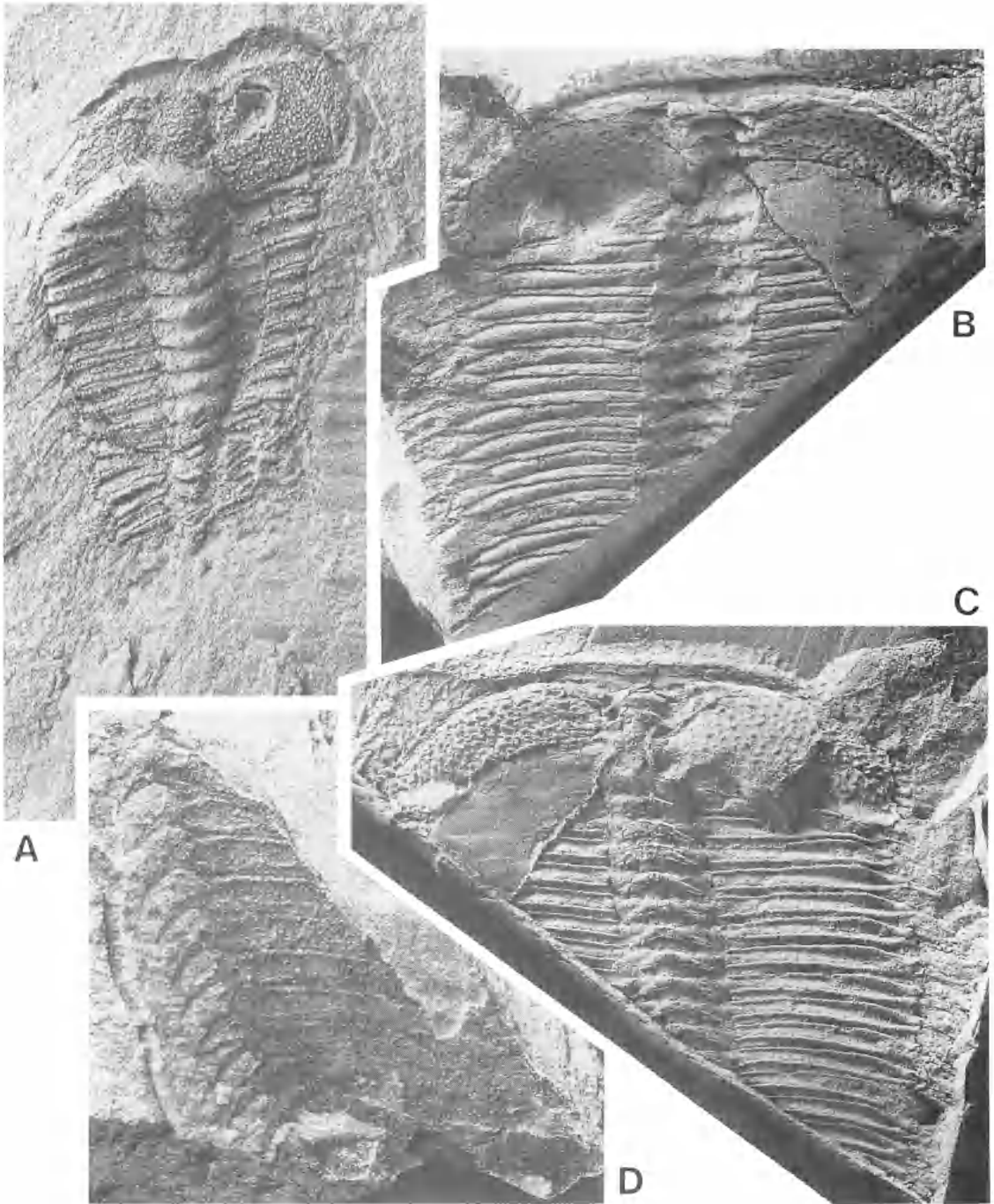


Fig. 2A-C. *Ivshiniellus briandailyi* nov. sp.: A, holotype SAM P24321, with anterior glabella relatively well preserved and composite mould of hypostome present, $\times 3$; B, C, paratype SAM P24844, B, external mould and C, silicon rubber cast of individual made from mould, both $\times 1.5$. D, conocoryphid gen. et sp. indet, SAM P24845, fragment photographed under a film of water, $\times 1.5$.

sufficient additional morphological information to justify formal description of the taxon.

The arthropod traces in near association with the body fossil specimens of the trilobites are of especial interest as the host rock represents a 'black shale' facies. Thus the traces provide an unusual palaeobiological perspective on this interesting find.

The studied specimens are registered in the Palaeontology Collection of the South Australian Museum, Adelaide (SAM).

SYSTEMATICS

Superfamily CONOCORYPHACEA Angelin, 1854

Family CONOCORYPHIDAE Angelin, 1854

Remarks: Divisions amongst the various genera of conocoryphids tend to be ill-defined due to description of cranidia alone or because many remains of these thin-shelled trilobites are markedly distorted. Furthermore, workers have tended to stress that the group is polyphyletic (Westergaard 1950; Szalay 1961; Hutchinson 1962; Rasetti 1967). On the basis of the evident positioning of the facial suture on the brim, the present form is a 'true' conocoryphid (Figs 2 & 4).

The family Conocoryphidae is rare in the Early Cambrian and much more common globally in the Middle Cambrian (Korobov 1973). Lochman-Balk & Wilson (1958) considered that the blind Conocoryphidae and Fodiscidae were characteristic of extracratonic, eusinic biofacies in the Cambrian of eastern North America and suggested that the blind condition was favoured by some important ecological factor.

Genus *Ivshiniellus* Korobov, 1966

Remarks: The better preserved of the original specimens (SAM P24321) is described as having a rearwardly directed furrow on the side of the anterior part of the glabella (Jago *et al.* 1984); medially this part of the glabella seems to have been entire and undivided. Though the front of the glabella of the new specimen is crushed, there appear to be four pairs of glabellar furrows (Fig. 3); the glabella tapers anteriorly and is somewhat constricted at about a third its length. These characteristics and other aspects of the cranidium conform to the diagnosis of the Early Cambrian genus *Ivshiniellus* Korobov, 1966. Most Cambrian conocoryphid genera show three pairs of glabella furrows (in advance of the occipital groove). The distance the glabella reaches forwards towards the frontal border, the possible presence of a raised pre-glabella lobe, and the width of the frontal field, if it is developed, are some of the significant character-

istics important for distinguishing conocoryphids.

While Korobov (1966) compared his new genus with the Middle Cambrian taxon *Bailliella* Mathew, 1885, it is similar to the Early Cambrian *Pseudatops* Lake, 1940. Species of *Pseudatops* may show four pairs of glabella furrows, but the glabella is only weakly tapered forwards and differs from that in *Ivshiniellus* in encroaching on the frontal border,

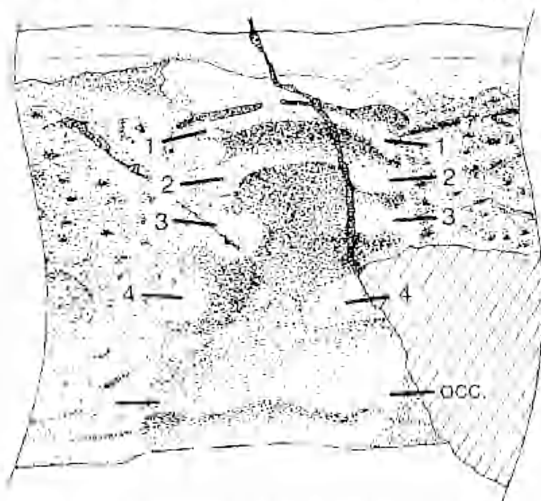


Fig. 3. Representation of the glabella and central part of the cranidium of SAM P24844 showing position of the four pairs of glabellar furrows, 1-4, in advance of the occipital furrow, occ. The more anterior glabellar lobes are strongly compressed in an anterior-posterior direction. Compare with Figure 2B.

Ivshiniellus briandailyi sp. nov.

FIGS 2-4

Conocoryphid sp. indet. Jago *et al.* 1984, pp. 208-210, figs. 2a-c.

Etymology: Honouring the late Dr Brian Daily (1931-1986) for his contribution to Australian geology and teaching.

Diagnosis: Brim weakly inflexed medially, cranidium encircled by border furrow and rather evenly covered by fine to coarse, pointed granules (spinules) in immature specimens, glabella almost smooth in more mature examples; pleura with acicular, weakly deflexed terminal spines; eleventh segment macropleterous.

Material: Holotype SAM P24321, lacking rearmost parts (Jago *et al.* 1984, fig. 2a, b); two paratypes, SAM P24322, rear thoracic segments and fragmentary pygidium (Jago *et al.* 1984 fig. 2c); SAM P24844, cranidium and parts of 14 thoracic segments.

Description: It is unnecessary to repeat the descriptions of the holotype and second fragment

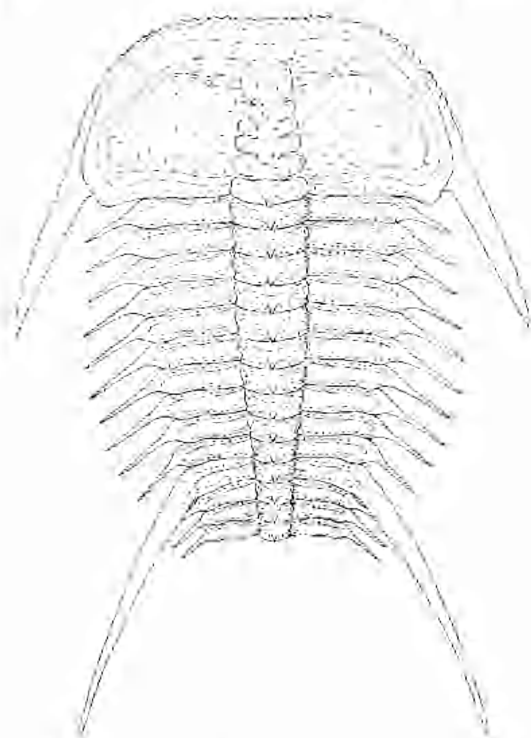


Fig. 4. Reconstruction of cephalon and major part of thorax of *Iyshiniellus briandailyi* sp. nov., about 2.5 times dimensions of holotype.

provided in Jago *et al.* (1984, pp. 209-210). The new specimen confirms the arcuate shape of the cephalon before, and slight median inflexion of the border, as well as indicating that the facial suture is confined to the brim. In the holotype, the granulose brim is poorly preserved and is wider than might seem obvious in the previously published figures; its posterior is well defined and the wide border furrow more finely and sparsely granulose than the central parts of the cranidium. The new remains show a nearly smooth, narrow glabella tapering forwards, with four pairs of glabella furrows directed rearwards. The fragmentary base of an occipital spine is present in the holotype.

The additional individual indicates at least 14 thoracic segments and confirms that the eleventh is macropleurous. The thin pleural ridges on the holotype show a line of 10-11 spinules or pointed granules on the anterior segments and 8-9 such granules on the posterior ones; other fine granules occur between.

Measurements: The holotype, SAM P24341, indicates an animal exceeding 25 mm in length. The distorted cranidium of SAM P24844 is 50 mm wide and the maximum width of the glabella is 8.5 mm; fourth thoracic segment about 1/45 mm wide,

excluding the spines and with the axis about 0.21 the width of the segment; animal in excess of 55 mm long.

Comparison: The genus includes two previously described forms, *Iyshiniellus nikolii* and *Iyshiniellus patulus* Korobov, 1966, both from the Aldanian Stage in Tuva, southeastern Siberia, within the Ezim Suite on the Ezim River. Both are represented by distorted cranidia and so any comparison with the present distorted remains must necessarily lack precision. *I. briandailyi* resembles *I. nikolii* in the shape of the cephalon, save for the distinctive medial inflexion of the frontal border; the glabella also seems narrower. *I. patulus* differs from both of the former in its pointed glabella and the somewhat quadrate shape of the fixed cheeks.

Mr J. G. Gehling has kindly provided photographs of cranidia and loaned several nearly complete dorsal exoskeletons of conocoryphid trilobites collected from the Parara Limestone at Bunyeroo Gorge in the Flinders Ranges. This material is of a taxon different to *I. briandailyi* as the eighteenth thoracic segment is macropleurous (not the eleventh, and the medial thoracic segments have remarkably long and strong pleural spines. The rather long glabella, which reaches a depressed border furrow behind the medially widened border, has three pairs of incised, backwardly directed furrows and a weak pair of depressions on the extreme anterior portion; laterally, the facial sutures cut off the major part of the brim. In its cephalic characteristics this form from the Parara Limestone shows similarities to the Early Cambrian genus *Atops* Emmons, 1844.

Conocoryphid gen. et sp. indet.

Remarks: The additional fragmentary thorax (SAM P24845) does not show the eleventh segment (counted from the most anterior segment preserved) macropleurous, and the pleural spines are more deflexed and evidently shorter than in the preceding form. However, the pleura show the characteristic wide-flat pleural grooves and narrow pleural ridges of conocoryphids. The thoracic segments are about 11.3 times as wide as long, excluding the spines, with the axis about 0.24 the width of the segment. The poor preservation has largely obliterated any surface detail.

Disarticulated thoracic segments associated with cranidia of *Ctenocephalus* Hawle & Corda, 1947, in material from the Middle Cambrian of France, show the pleural terminations narrowed abruptly and thence produced into a somewhat deflexed, slender spine. The shape of the pleural terminations in SAM P24845 is markedly similar. This specimen could be a dimorphic individual of *I. briandailyi*

or even represent a separate conocoryphid taxon, but basically is too fragmentary for determination.

Age of trilobite finds

The occurrence of *Ivshiniellus* on the Fleurieu Peninsula is of potential significance with respect to the timing of a major stratotectonic development within the Adelaide Fold Belt. Cambrian rocks of the Normanville Group below the Heatherdale Shale are of both basinal and shelf aspect (Daily 1963, 1976; Jago *et al.* 1986). The trilobites occur in the upper member of the Heatherdale Shale high in the section of the formation exposed (Jago *et al.* 1984). At Carrickalinga and more southerly parts of the Fleurieu Peninsula the Heatherdale Shale is abruptly succeeded by up to ca. 1300 m of turbidites of the Carrickalinga Head Formation (*sensu lato* of Daily & Milnes 1971, 1972; Milnes 1986), the basal interval of the thick psammitic and/or pelitic sediments of the Kanmantoo Complex. Sandstones of subtidal or tidal origin (Backstairs Passage Formation) succeeding the Carrickalinga Head Formation record a phase of basin filling. Jenkins (1989) identifies this overall basinal deepening and shallowing as the 'Ramindjeri/Jadlauria stratotectonic cycle' and the organic-rich sediments (Foster *et al.* 1985) of the Heatherdale Shale may be considered as the 'eustatic' phase marking the start of rapid subsidence associated with renewed lithospheric extension.

The likely age of *Ivshiniellus* in Siberia is late Aldanian (Korobov 1973; Jago *et al.* 1984) or medial Early Cambrian, and the comparable genus *Pseudatops* also occurs in the ?mid Early Cambrian of eastern North America and the British Isles. The present finding that *I. hriandailyi* and a conocoryphid from Bunyerroo Gorge are different taxa weakens the claim of Jago *et al.* (1986) that conocoryphids suggest a correlation between the Heatherdale Shale and higher parts of the Parana Limestone in the Flinders Ranges, though on a tectonic basis the onset of deposition of the dark, nodular offshore facies of the latter formation may well have corresponded with the deepening signalled by the Heatherdale Shale (see Jenkins 1989).

Trace Fossils

An upper-surface bedding plane at the trilobite site shows a relatively well preserved arthropod trail extending over a distance of 80 cm, parts of two other trails probably made by large trilobites and a poorly preserved section of the back-filled burrow produced by a worm-like creature (Figs 5-6). This surface has been preserved due to an unusual circumstance.

The arthropods evidently moved over a relatively fine-grained and soft, muddy substrate with the ends of their limbs making deep impressions. Had this surface been subsequently buried by further silt, the cleavage now present in the rock due to deformation (Cambro-Ordovician Delamerian Orogeny) would probably preclude splitting along the particular bedding surface. However, the traces were buried by a 3.5 cm thick bed now comprising intergrown phyllosilicates and minor fine (-0.1 mm diameter), angular quartz grains, which are commonly amalgamated and show undulose extinction. The quartz is probably detrital. XRD analyses of the rock confirm visual observation that the bed is inhomogeneous with a (less weathered?) fraction comprising predominantly illite 2M₁, minor muscovite M₁, and kaolinite-smectite, and a second (weathered?) fraction including illite and Ca montmorillonite. Iron rich opaques are concentrated in parts. Illite 2M is consistent with a paragenesis involving deep burial and alteration of possible older mineral phases. The bed is continuous along strike over an exposure distance of 60 m and thickens slightly towards the south (up to 4.5 cm). In places, obvious granular components that are apparently 'relicts' of the original sedimentary particles grade in size from ~ 0.5 - 1.2 mm near the base of the bed to ~ 0.1 mm at the top.

The granular aggregates of phyllosilicates possibly represent the highly altered components of an air-fall tuff that mixed with a small amount of detrital material and formed a slurry which buried and moulded the trilobite traces. During modern weathering a line of parting developed subjacent to the underlying siltstone such that a very thin veneer of granular material still adheres to and completely covers the traces.

The trail traced over 80 cm consists of sub-parallel rows of rather closely spaced imprints of ambulatory limbs and averages 75 to 80 mm in width. The individual imprints tend to be set obliquely or en-echelon and the best preserved are about 10 mm long. This trace is of the form illustrated by Seilacher (1955, fig. 1a, b) and was evidently made by a perambulating trilobite with its body axis aligned in the direction of travel. In one area it is overlapped by a crudely segmented trace made by a worm-like animal. Nearby exposures in the Heatherdale Shale show much better preserved examples of what is probably this same trace occurring in association with numerous burrows of a relatively large form of *Planolites* Nicholson, 1873. The segmented trace is probably of endogenic origin and well preserved examples show a regular back-filling of large ovate faecal pellets arranged transversely.



Fig. 5. Bedding plane below tuff horizon, showing trace fossils made by trilobites, A-C, and structure, D, attributed to an unknown worm-like animal. A-A', trace made by perambulating trilobite with body aligned in direction of travel; B-B', marks made by large trilobite moving obliquely; C-C', indication of a trilobite travelling relatively quickly. Scale bar equivalent to 20 cm.

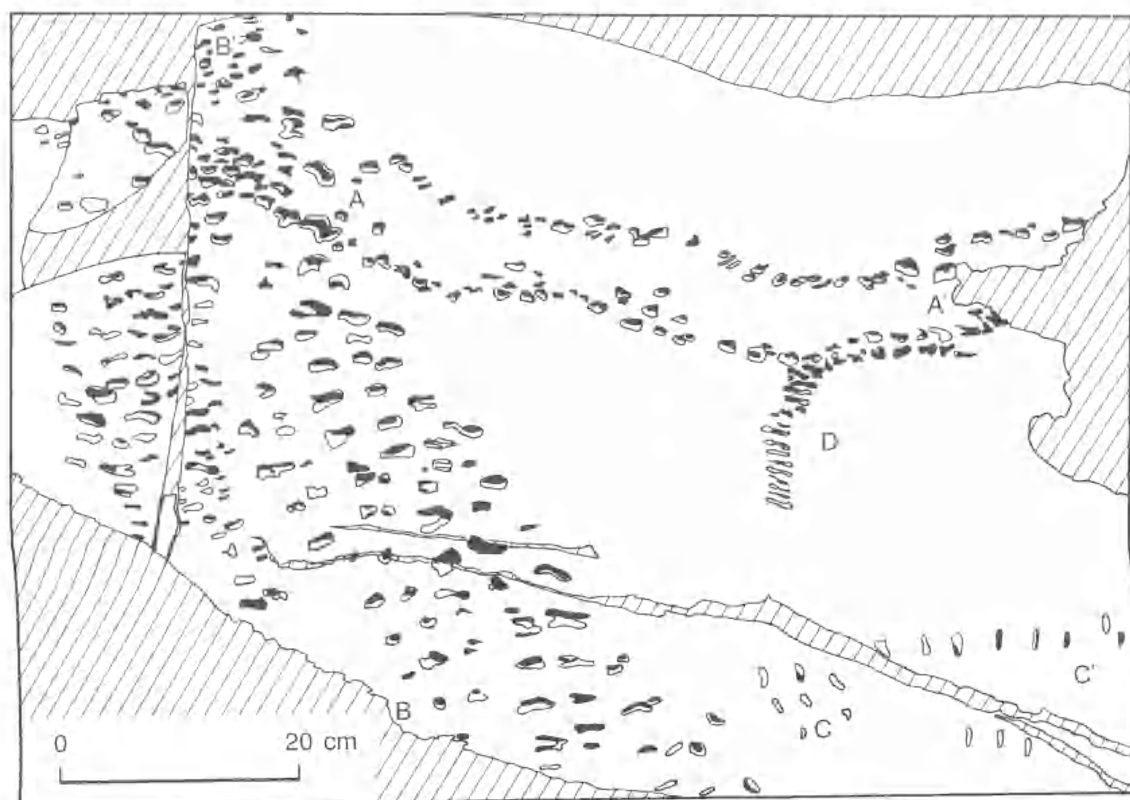


Fig. 6. Representation of bedding surface portrayed in Fig. 5 indicating the several sets of markings made by trilobites (A-A', B-B', C-C') and another unknown animal (D).

The two other traces show relatively widely spaced series of imprints interpreted as the impressions of the tips of the telopodites of trilobites. In the larger trace, the individual imprints are up to 20 mm long and on one side of the complete trail are arranged in rather irregular rows positioned in an en-echelon manner. This sort of marking is well explained by Seilacher (1955, fig. 1) and indicates a trilobite moving obliquely crab-wise, perhaps partly in response to a gentle side current. The tips of the limbs which formed the marks on either side of the trace spanned approximately 23 cm, indicating a quite large animal. The imprints of the remaining trace are widely spaced and suggest a smaller animal travelling relatively quickly with the body aligned in the direction of travel. These marks are not especially distinctive (and were only seen in certain lighting) but are comparable with some of the large trilobite trails occurring in the late Early to Middle Cambrian Kangaroo Island Group of Daily (1956), on the north coast of Kangaroo Island.

The body fossil remains of the trilobites described herein occurred respectively 1.6 m stratigraphically below the surface with trilobite trails (SAM P24844) and 88 cm above this surface (SAM P24845). The traces suggest that trilobites were live inhabitants of the bottom environment.

Palaeobiological significance

The thinly laminated argillites of the upper member (~240 mm thick) of the Heatherdale Shale are almost entirely flat bedded and certainly accumulated at depths below storm wave base (cf. Jago *et al.* 1986). A single rippled surface observed may reflect localised bottom currents. Considering the thickness of the succeeding turbidites, the depth of water in the depositional environment was probably of the order of hundreds of metres.

Jago *et al.* (1984) cite and illustrate apparent mudcracks in the Heatherdale Shale (their fig. 4) as possibly indicating a shallow environment of deposition but they concede that the cracks may have formed due to syneresis. Dziński & Walton (1965) illustrate (their figs 112 & 113) comparable cracks in turbidites.

Trilobite trails occur abundantly in parts of the late Early to Middle Cambrian sequence on the north coast of Kangaroo Island (Sprigg 1955; Daily *et al.* 1979). Examples of such trails up to 10–12 cm in width are especially numerous in intervals of these rocks deposited in tidal and subtidal facies. This association of trilobite trails in shallow-water sediments is common world wide during the older Palaeozoic and constitutes the *Cruziana* facies of Seilacher (1964). Thus it is apparent that trilobites

had an ordinary oxidative kind of metabolism such as is characteristic of modern, free living arthropods and metazoans in general.

The arthropod trails in the Heatherdale Shale suggest relatively large animals moving over the bottom in some numbers. The implication is that the body fossil remains of trilobites were part of an indigenous population and not isolated individuals somehow transported into the environment by chance. Presuming an oxidative metabolism for the trilobites, and the worm-like creatures responsible for various burrowed horizons, the bottom waters of the Heatherdale Shale environment were clearly not uniformly anoxic and must have been at least moderately well oxygenated at the times of bioturbation. This contradicts the commonly held opinion that black shales characterize oxygen starved basins; fluctuating oxygen tensions may be more likely (Morris 1980; Kaufman 1982; Küspert 1982; Wetzel 1982; Conway Morris 1985).

By measuring the displacement of a conveniently sized plaster model of a trilobite, the soft tissue mass of the animal which made the 23 cm wide trail may be estimated at ~500 g. With reference to fig. 8.6 of Alexander (1979), the oxygen consumption of an animal of this size may have been about 0.045 ml gm⁻¹ hr⁻¹, or for the whole organism, 23 ml hr⁻¹. Runnegar (1982) demonstrated that the surface area of the respiratory organs (e.g. gills) of aqueous animals is approximately proportional to the body mass; this suggests a respiratory exchange surface of ~500 cm² for the trilobite. Application of equation 13.5 of Alexander (1979, p. 279) indicates that the partial pressure between the sea water and blood over the respiratory surface needed to supply the required oxygen consumption is ~0.06 atm. Assuming that the respiratory pigment in the animal's blood was saturated at 0.02 atm, the minimum oxygen concentration in the sea water necessary for the trilobite was ~0.08 atm or ~38% PAI (~60 mm Hg of O₂). This value lies within the medial part of the spectrum of oxygen concentrations in the oxygen minimum layer of modern oceans, effectively 2.5% PAI to 60% PAI (Barnes & Hughes 1982, fig. 1.9).

There is currently a renewed wave of speculation concerning the possible increase of atmospheric oxygen during the late Precambrian and its relationship to the emergence of the metazoa and higher plant life (Runnegar 1982a, b and pers. comm.; Glaessner 1983, 1984). The present example suggest that simple observation of dark coloration in parts of Precambrian sequences (e.g. grey and black phyllites in the 'Torrensian' Series of the Adelaidean) is unlikely to give reliable information on ambient oxygen tensions. The coloration of

shales will also reflect diagenetic processes and the effects of incipient metamorphism; for example recrystallization of haematite to specularite may cause beds to become almost black (Clemmey & Badham 1982).

I. brundailyi is remarkable for the long genal spines, the attenuated spines on the pleurites and its macropleurite eleventh segment. Similar long spines in odontopleurid trilobites have been considered to have functioned in helping to support the animals on the sea bottom, either during 'resting' or while they were feeding with the aid of currents passing between the substrate and the lower side of the thorax (Wittington 1956a, b; Clarkson 1969; for a different opinion see Bergström 1973). Such an adaptation is consistent with *I. brundailyi* inhabiting a soft muddy bottom. Because of the

lack of streamlining brought about by the spines the trilobite was probably not an agile swimmer, and this accords with the finding of trackways in close proximity to its remains. However, the trackways indicate larger animals than the body fossil specimens and there is no way of telling whether the traces were made by more mature individuals of conocoryphids or other trilobites known to reach large size locally, such as *Redlichia* Cossmann, 1902 (see Conway Morris & Jenkins 1985). A host of modern day creatures have adapted to inhabit caves and other dark places and become secondarily blind, and loss of sight in conocoryphids would have posed no disadvantage if these primal denizens of the deep were bottom dwellers who lived below the effective penetration of light, sustained primarily on settled detritus.

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